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INTERPOPULATION VARIATION IN THE COLUBRID SNAKE *NATRIX PRYERI* FROM THE RIUKIU ISLANDS, WITH DESCRIPTION OF A NEW SUBSPECIES

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Introduction

Studies by one of us (Munsterman) of the reptile fauna of the Riukiu Islands and by the other (Malnate) in the systematics of the Asian species of the snake-genus *Natrix* quite naturally crossed at the species *Natrix pryeri*. *Natrix pryeri* is isolated in its relationship with its congeners and is the sole representative of *Natrix* inhabiting the Riukiu Islands. Under these circumstances the combination of our resources in a single report on the species should, it is hoped, be of greater value than that which would have resulted from our individual efforts.

Natrix pryeri was described by Boulenger in 1887. Little attention has been paid the species although the number of specimens available for study has increased in the intervening years since its discovery (unfortunately,

ecological and natural history data did not increase to the same degree). For this study 84 specimens have been examined; data on 25 additional specimens have been obtained from literature and colleagues. These 109 examples are distributed through the Riukiu island chain (from north to south) as follows: Amami, 31; Kikaiga, 3; Okinawa, 52; Miyako, 2; Ishigaki, 9; Iriomote 1 (5 specimens are labeled "LooChoo Islands," without more specific data; four specimens in the collections of the Senckenberg Museum are labeled "Miyama," a locality unknown to us; two specimens are of questionable derivation). Wall (1905) examined 57 specimens, mostly from Okinawa, in the collection of A. Owston, Yokohama, Japan, but made only the briefest possible mention of the species in his notes. The present whereabouts of this collection is unknown.

Systematic Discussion

Natrix pryeri (Boulenger).

Tropidonotus pryeri Boulenger, 1887, Proc. Zool. Soc. London, 1887, p. 149, pl. 18, fig. 3 (type locality: Loo Choo Islands, herein restricted to Okinawa); 1893, Cat. Snakes Brit. Mus. (N. H.), vol. 1, p. 250.

Natrix pryeri, Stejneger 1907, U. S. Nat'l Mus. Bull. 58, p. 284, pl. 20, figs. 247–249; Maki, 1931, a monograph of the snakes of Japan, p. 40 pl. 10, text-figs. 15–16.

Scutellation. Rostral broader than high, narrowly visible from above. Internasals subrectangular, longer than wide, rarely long as wide; internasorostral contact (ratio between contact of a single internasal with the rostral and that of an anterior nasal with the rostral) less than 1 or 1. Prefrontals as wide as long or slightly wider (fused in two specimens), slightly longer than internasals, in contact with supraoculars. Frontal longer than wide l/w = 1.4–1.8 [mean 1.6; 20 specimens]), longer than its distance from snout tip, equal to or slightly longer than length of interparietal suture. Parietals longer than combined width, posterior angle acute. Nasals divided, nostril between two plates. Loreal longer than high, rarely as long as high. Preoculars 1, rarely 2; postoculars 3, rarely 4 or 2. Anterior temporals 2, rarely 1; posterior temporals 2, frequently 1, rarely 3. Supralabials 8, rarely 9 or 7; fourth and fifth (rarely fifth and sixth, fourth only, or third and fourth) border orbit; seventh largest. Infralabials 10, rarely 9 or 11; 5 (rarely 6) border anterior chin-shields. Posterior chin-shields longer than anterior pair, separated from one-third to entire length by small scales. Dorsal scales in 19–19–17 rows, keeled, those of outer row less strongly so; apical pits prominent throughout body length; number of scale rows reduced by loss of fourth scale row (between 60.2–68.1% [mean 63.9%] of head and body length [11 males]; 58.1–81.4% [mean 65.1%; 23 females]). Ventrals 167–188 (172–188 [mean 178.9; 34 males]; 167–182 [mean 174.1; 52 females]); anal plate divided; subcau-

dals 94–133 (102–133 [mean 117.2; 19 males]; 94–126 [mean 113.2; 28 females]).

Color. Dorsum grayish or brownish. Anterior part of body with series of elongate, dark lateral blotches which meet in opposition or slightly alternate at vertebral line; blotches separated by broad yellowish interspaces; scales of interspaces sometimes have dark tips, or interspaces may be reduced to sharply defined, dark-edged, light vertical bars extending from ventrals to or near to vertebral line. On posterior portion of body light areas are reduced to dorsolateral series of light spots on the fourth through sixth scale rows; dark blotches are also reduced forming small black spots below each light one and sometimes also evident as paired squarish black spots or irregular transverse bars across back. Irregularly on dorsum dark scales may be finely edged with white. Head blackish or light brown, usually mottled or marbled with gray or white (marbling may be obscure or lacking); paired parietal light spots commonly present but often obscure; short postparietal light streak present, may be reduced to a spot at end of interparietal suture. Supralabials whitish, sutures between first to sixth shields edged with black; on larger (older) specimens supralabials anterior to eye may have suffusion of dark color across upper edges; broad band present from eye across seventh and eighth supralabials to angle of jaw, there joining forward extension of first body blotch; light color of seventh supralabial is confined to lower anterior corner of shield; on eighth supralabial light color is restricted to a central spot. Nape black; well-defined yellowish nuchal crescent present on each side, these joining at vertebral line and extending posteriorly onto neck for varying distances forming Y-shaped mark; this mark may be reduced to a light spot at angle of jaw and a very short-branched "Y" vertebrally or may rarely be absent. Infralabials whitish, a few anterior shields with narrow black edges. Venter yellowish, dorsal color encroaching onto outer edges of ventrals; a series of small, black spots present along lateral edge of belly, these usually irregular or absent anteriorly, becoming stronger posteriorly and subcaudally, sometimes forming continuous line.

Measurements and proportions. Total length: largest male, 987 mm., plus (tail docked); largest female, 1095 mm. Tail/total length ratio: 0.273–0.345 (0.273–0.337 [mean 0.306; 18 males]; 0.284–0.346 [mean 0.311; 23 females]). Head length/body length ratio: 0.037–0.053 [mean 0.044; 46 specimens]; head length/width ratio: 1.7–2.3 [mean 1.97; 50 specimens]; snout (tip to level of midorbital point) 30–38% of head length (32–38% [mean 35.6%; 19 males]; 30–38% [mean 33.5%; 35 females]); eye diameter, if projected forward from anterior rim of orbit usually reaches midnostril point, distance varying from middle posterior nasal to middle anterior nasal (ratio eye diameter/head length: 0.15–0.23 [mean 0.177; 54 specimens]).

Dentition. Maxillary teeth 23–29 (32 counts), last two teeth strongly enlarged (occasionally only slightly larger than preceding teeth). Palatopterygoid series of teeth 35–45 (11–17 palatine plus 25–30 pterygoid teeth [9 specimens]), gradually decreasing in size posteriorly. Dentary teeth 22–35 [12 specimens], subequal or somewhat larger anteriorly.

Hemipenes. Hemipenes unforked, short, extending to level of fifth-eighth subcaudals; spinous, distal spines small, basal spines stouter; one strongly enlarged basal spine, followed distally by small group of stout spines; organ base furrowed. Sulcus spermaticus single, extending to organ tip, lips spinous.

Distribution. Known only from the Riukiu Islands (Oshima group: Edateku, Kakeroma, Kikaiga, Amami, Uke, Tokuna, Okierabu; Okinawa group: Okinawa; Miyako group: Miyako; Yaeyama group: Ishigaki, Iriomote).

Natural history. The topography of the Riukiu Islands varies from relative flatness to low mountains. The Oshima group is the most rugged (greatest elevation, 2,300 feet); Okinawa is mountainous in the north (highest peak, 1,557 feet), plateau-like in the south; Miyako is low and flat; the Yaeyama Islands are mountainous with limited tableland (maximum elevation, 1,680 feet).

Vegetation is subtropical. Broadleaf trees are found at sea level; evergreens are characteristic of the mountain slopes. The lowlands are extensively cultivated, the chief crops being rice, sweet potatoes and sugar cane. The flora of the northern islands is most closely related to that of southern Japan, while the southern islands are rich in subtropical elements related to those of Formosa.

Professor Kazuo Koba *(in litt.)* informs us that on Amami and Okinawa *N. pryeri* is common in the rice fields and grasslands near the hills, and also is found in the forests. "*Natrix pryeri* and *Liopeltis* [= *Opheodrys*] *semicarinata fritzei* are most common species among the snakes of Amami-ôshima." Examination of the stomach contents of all specimens seen yielded frogs only, *Rana limnocharis* being the only species identified.

Wall *(op. cit.)* notes four females with eggs. Two contained three eggs, one five and one six. The eggs varied in size from 0.9 to 1.8 inches long by 0.5 inches in diameter. Two eggs were found in the ovaries of one female examined, another contained four. These were approximately of the size noted by Wall.

Sexual variation. As indicated in the descriptive data for the species sexual variation is not highly developed in *N. pryeri*. Average differences in some characters are defined. The number of ventrals and subcaudals average higher in males; females appear to attain a somewhat greater length; the

fourth scale row on the body extends for a greater mean length on females. Except for the higher number of ventrals in males these characteristics are typical variations found between the sexes in colubrid snakes. Peculiarly, the proportionate length of the tail is about equal in both sexes.

In addition to these variations, male *pryeri* exhibit certain characters not found in females. The scales of the snout (occasionally all dorsal head scales) are tuberculate on males of over 375 mm. body length (lower limit estimated on the basis of two males, 383 and 414 mm. body length, which show the character poorly defined). On some males the scales of the anal region may bear swollen keels or the apical scale pits in the same area may be much more pronounced (visually, they appear to be swollen or tuberculate in form) than elsewhere on the body. It is presumed that these characters are related to sexual activity but without knowledge of the courtship and mating habits of the species verification is impossible.

GEOGRAPHICAL VARIATION. Differentiation of the populations of *N. pryeri* inhabiting the various islands of the Riukiu archipelago is evidenced by their variation. Interpopulation variation can best be presented by considering each population in turn, from north to south. Standard scale characters and proportions are shown in table I and the interpopulation variation in certain of these is illustrated on the accompanying graph (fig. 1). Other characteristics observed are noted below.

Amami. A distinguishing characteristic of the Amami population is the strongly defined marbling of the head with light gray in contrast with other populations wherein the marbling is either obscure (dark gray) or absent. Males from Amami show a strong development of the apical pits in the anal region (swollen keels on these scales have not been noted). The fact that 8 of 13 specimens examined have the posterior chin-shields separated their entire length by small scales is of unknown significance but in no other population is this feature so predominant. A further peculiarity of this character is that the specimens on which it occurs are all males, and those individuals with less than complete separation (½ to ¾) are all females.

Kikaiga. The population of *N. pryeri* occurring on this island is known from three specimens only. These are generally lighter in ground color than the other populations; verification that this is a natural condition and not the result of preservation techniques is desirable. It is reasonable to assume that additional data will associate the Kikaiga population with that of Amami.

Okinawa. There is a strong tendency in this population toward increase in the number of posterior temporals. Half of the specimens studied (26 of 52) have two posterior temporals on both sides of the head, an additional eight have two on one side only. Two posterior temporals occur in only five

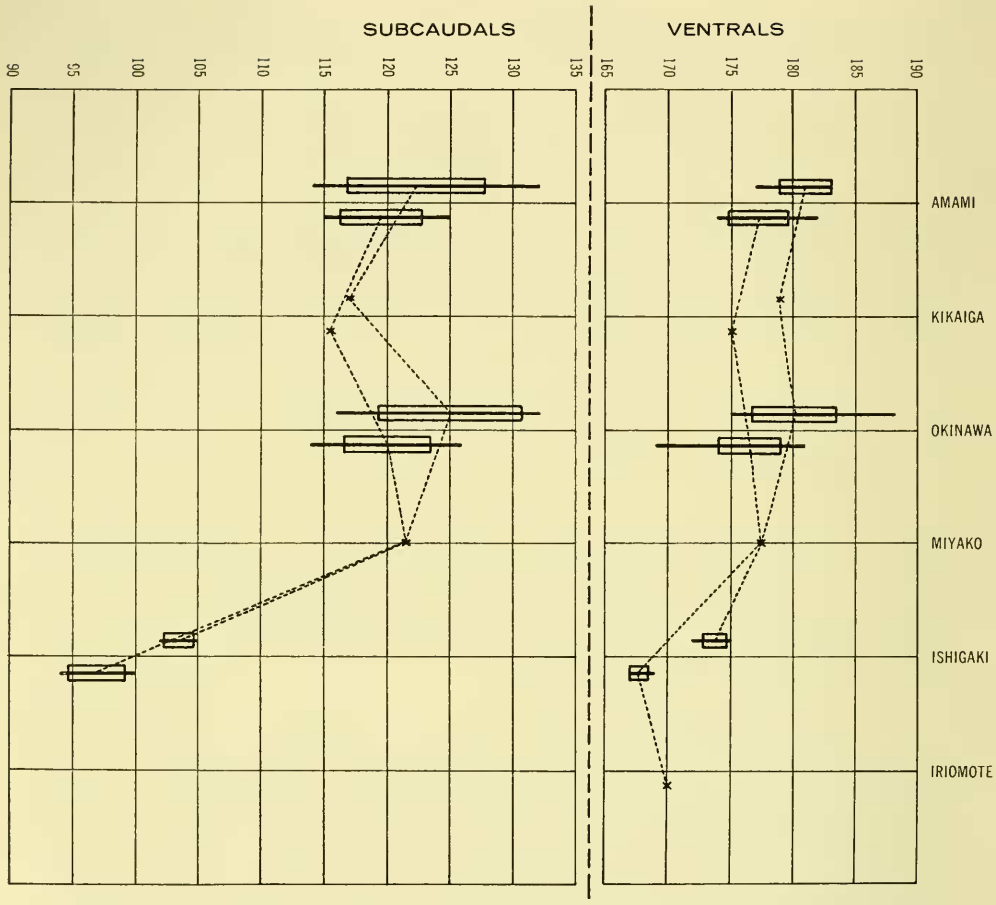

Figure 1. Known variations of ventrals and subcaudals (sexes separate), within populations of *Natrix pryeri*. Dotted line connects means of the same sex in each population. Open boxes show one standard deviation from the mean.

other specimens throughout the remainder of the range. In addition, it is noted that among the specimens with a single posterior temporal only one is a male showing the condition on one side only; all the others are females. The significance of this is unknown. In this population the nuchal crescent shows consistent reduction. Many individuals have only a light spot at the angle of the jaw and the forks of the Y may be reduced or even lost. Lateral spotting on the ventrum also shows reduction, being absent on the anterior portion of the belly to a greater extent (one-half) than in any other population. Okinawan males have swollen keels and pronounced apical pits on the scales of the anal region.

The four specimens in the Senckenberg Museum (numbers 17629–32) labeled "Miyama" have not been seen by us but certain data of scutellation

have been supplied by Dr. Klemmer. Three are adult females, one is of unknown sex. Ventrals and subcaudals (in the three females) number 176–183 and 119–125 (2 only), respectively. Temporals are noted as being 2 + ?, 3 + 2, 2 + 4, 4 + 3; preoculars 1, postoculars 3, supralabials 8 in all individuals. On the basis of the scale counts, especially the high number of temporals, it is assumed that the specimens are from the Okinawa group.

Miyako. Natrix pryeri is known from this island by only two specimens. In addition to the data shown in the chart it is reported to us by Dr. Klemmer *(in litt.)* that the ventral spotting on these specimens is very distinct on all ventrals.

Ishigaki. The pattern of the Ishigaki population is unusual and most distinctive; the light interspaces on the anterior portion of the body, broad in other populations, are reduced to narrow, dark-edged vertical bars; the head and occipital region are uniformly light-colored, in great contrast with the very dark head usual to the species elsewhere. In this population are found the lowest ventral and subcaudal counts of the species; also, both characters exhibit stronger sexual differentiation than in any other population (available data show no overlap of counts between the sexes in either character). Male specimens of *N. pryeri* from Ishigaki have been noted to bear swollen keels and strongly produced apical pits on the scales of the anal region.

Maki (1931) lists Ishigaki in the range of *N. pryeri* (the "Tshigaki" listed in his chart of scutellation ?) but the count of ventrals (183) and subcaudals (115) are both high for the Ishigaki population as otherwise known to us. Maki makes no comment as to pattern (an obvious and noteworthy distinction). We do not include this specimen in our description of the population.

Iriomote. Known only from a single specimen described by Stejneger *(op. cit.)*. Stejneger describes the anterior light interspaces as "vertical bars" and thus suggests a similarity between this population and that of Ishigaki. In this regard mention must be made here of a specimen (CAS 21920) reportedly from Ishigaki. In its dorsal body pattern it compares well with Ishigaki specimens and Stejneger's Iriomote example. The head, however, is dark, marbled with dark gray; the supralabials are heavily mottled with dark; the nuchal crescent is reduced to light spots at the angles of the jaws. On the ventrum there is a heavy development of melanophores: the chin and throat are mottled with black; the ventral spots are boldly developed, beginning at the gulars, and the area between them and the sides is strongly suffused with the dark flank color; the subcaudal surface is heavily powdered gray. Scutellation is generally normal except that the ventral count (165) is the lowest known (unfortunately, the tail is docked and a subcaudal count cannot be determined); two posterior temporals are pres-

TABLE I

Sex	*Amami*	*Kikaiga*	*Okinawa*	*Miyako*	*Ishigaki*	*Iriomote*
M	177–183 (13) 181.0 ± 2.11	179 (1)	175–188 (18) 180.2 ± 3.37	176–179 (2) 177.5	172–175 (4) 173.8 ± 1.09	
F	174–182 (18) 177.3 ± 2.36	174–176 (2) 175	169–181 (31) 176.5 ± 2.46		167–169 (5) 167.6 ± 0.80	170 (1)

TABLE II

M	114–132 (6) 122.2 ± 5.54	117 (1)	116–132 (10) 125.0 ± 5.67	118–125 (2) 121.5	102–105 (3) 103.3 ± 1.25	
F	115–125 (11) 119.6 ± 3.20	115–116 (2) 115.5	114–126 (13) 120.1 ± 3.43		94–100 (4) 97.0 ± 2.24	

TABLE III

M	.309–.320 (5) .3116	.308 (1)	.298–.337 (10) .3184		.273–.286 (3) .2807	
F	.304–.326 (10) .3117	.311–.346 (2) .3285	.302–.338 (10) .3207		.284–.287 (3) .2850	

TABLE IV

M	62.7–68.1 (3) 64.5	62.2 (1)	60.2–66.6 (3) 64.0		63.6–65.2 (4) 64.8	
F	62.3–69.2 (5) 66.1	64.4–64.5 (2) 64.5	58.1–81.4 (13) 65. 9		61.8–65.9 (3) 63.9	

TABLE V

	Amami	*Kikaiga*	*Okinawa*	*Miyako*	*Ishigaki*	*Iriomote*
Labials	8/10 (24) 9–8/10 (1) 8/10–11 (1)	8/10 (3)	8/10 (43) 9–8/10 (1) 7–8/9–10 (1) 8/9–10 (1) 8/10–9 (1)	8/? (1)	8/10 (7) 9/10 (1) 8/10–11 (2)	8/10 (1)
Oculars	1, 3 (28) 1, 4–3 (1) 2, 3 (1) 1, 3–2 (1)	1, 3 (3)	1, 3 (47) 1–2, 3 (1) 2, 3 (1) 1, 3–4 (1)	1, 3 (1)	1, 3 (8) 1, 2–3 (1) 1, 3–4 (1)	1, 3–4 (1)
Temporals	2, 1 (27) 2, 2–1 (3) 2, 2 (1)	2, 1 (3)	2, 2 (24) 2, 2–1 (6) 2, 1–2 (2) 2, 1 (15) 1–2, 2 (1) 1, 1 (1) 2, 2–3 (1)	2, ? (1)	2, 2 (1) 2, 1 (8) 1, 1 (1)	2, 1 (1)

Table I.[1] Summary of variation in ventral counts in populations of *Natrix pryeri*.

Table II. Summary of variation in subcaudal counts in populations of *Natrix pryeri*.

Table III. Summary of variation in tail ratio in populations of *Natrix pryeri*.

Table IV. Summary of variation in persistence of the fourth scale row on the body in populations of *Natrix pryeri*. Figures are percentages of body length in which fourth scale row is present.

Table V. Summary of variation in head scales in populations of *Natrix pryeri*.

1. *Note:* In Tables I–II the mean and standard deviations from the mean are shown. In Tables III–IV only the mean is shown. The numbers in parentheses in all tables indicate the number of specimens from which variation was determined.

ent. The maxillary teeth number 31, the highest count recorded. On the basis of these data it may be assumed that this specimen came from the Yaeyama group but more likely Iriomote rather than Ishigaki.

Analysis of the interpopulation variation in *N. pryeri* demonstrates the development of certain patterns in the linear distribution of the species through the archipelago (see fig. 1 and tables 1–5).

1) Subcaudals are highest on Okinawa (means: male, 125.0; female, 120.1), are somewhat reduced on the more northern Amami (male, 122.2; female, 119.6), much reduced on the southern Ishigaki (male, 103.3; female, 97.0).

2) Ventrals appear to be correlated with the above, although the pattern is not so strongly defined (means: male, 180.2; female, 176.5, on Okinawa; male, 181.0; female, 177.3, on Amami; and male, 173.8; female, 167.6, on Ishigaki). Range of variation in ventrals seems to demonstrate the pattern more prominently (see figure 1).

3) Tail/total length ratio appears to follow the same trend (means: male, 0.318; female, 0.320, on Okinawa; 0.312 (both sexes), on Amami; male, 0.281; female, 0.285, on Ishigaki).

4) The length of the snout as a percentage of the head length varies in the same manner (means: male, 35.9; female 35.1, on Okinawa; male, 35.1; female, 32.9, on Amami; male, 34.8; female, 32.0, on Ishigaki).

5) Items 3 and 4 above are probably correlated with total length which shows a comparable trend but not so clearly demonstrated. The largest known specimens are from Okinawa, those from Amami and Ishigaki being smaller.

Overlying these broadly defined patterns are prominent local variations.

a) The strongly developed marbling of the head in the Amami population.

b) The predominance of two posterior temporals, and reduction of the nuchal pattern in the population inhabiting Okinawa. (The former may represent the pattern of variation outlined above.)

c) The peculiar pattern developments in the Ishigaki population: reduction of the anterior light dorsal areas and the development of a light head coloration.

Thus, two types of variation are associated with the distribution of *N. pryeri:* a basic variation in certain characters, presumably older and perhaps related to the initial dispersal of the species; and, local differentiations occurring in other characters, related to the discontinuities of distribution established by geophysical factors, and possibly due to the isolation of small units of the species continuum (Sewell Wright effect). It is not possible to

demonstrate adaptive or nonadaptive variations in the populations; however, it is assumed that both are involved.

Differentiation among most populations of *N. pryeri* is not great, except in regard to the inhabitants of Ishigaki. The unusual pattern developed in this population is combined with low ventral counts and an extremely low number of subcaudals. The history of the Yaeyama group is one of isolation, at times considerably greater than at the present (Hanzawa, 1935). In spite of the physical isolation of this population complete genetic isolation is not a certainty. Similarities in basic scutellation is believed to demonstrate a close association among populations in the past, if not in the present. *Natrix pryeri* on Ishigaki is sufficiently distinct to warrant systematic recognition; however, because of the considerable overlap in scale characters among all populations and because the degree of genetic isolation cannot be fixed recognition is limited to the subspecific level.

At the moment it is impossible to recognize the subspecies as occurring elsewhere than on Ishigaki; however, Iriomote has through its history been closely associated with Ishigaki (Hanzawa, *op. cit.*), and it may well be shown later that *N. pryeri* in the whole Yaeyama group should be considered a single taxon.

The population of *N. pryeri* inhabiting Ishigaki may be designated:

Natrix pryeri ishigakiensis Malnate and Munsterman, new subspecies.

Natrix pryeri (part ?). MAKI, 1931. A monograph of the snakes of Japan, p. 40.

DIAGNOSIS. A form of *N. pryeri* distinguished by a uniform, light-colored head; reduction of broad anterior light interspaces to narrow, dark-edged vertical bars; much reduced subcaudal count; shorter tail. Presently known only from Ishigaki.

HOLOTYPE. CAS 21913; adult male, collected on Ishigaki-shima, Yaeyama group, Riukiu Islands, by Victor Kühne, 25 May to 2 June, 1910.

PARATYPES (8). CAS 21914, 21917, 21919, males; CAS 21912, 21915, 21916, 21918, 21921, females; all collected on Ishigaki-shima, Yaeyama group, Riukiu Islands, by Victor Kühne, 25 May to 2 June, 1910.

DESCRIPTION OF HOLOTYPE. Rostral edge visible from above. Internasals longer than wide, internasorostral contact ratio equals one. Prefrontals wider than long, slightly shorter than internasals, in contact with supraoculars. Frontal longer than its distance from tip of snout, equal in length to interparietal suture, length/width ratio 1.4. Parietals as long as combined width, posterior angle acute. Nasals divided. Loreal longer than high. Preocular 1, postoculars 3. Anterior temporals 2, posterior temporals 1. Supralabials 8, fourth and fifth border orbit, sixth largest. Infralabials 10, 5 border anterior

chin-shields, sixth largest. Posterior chin-shields much the longer pair, separated entire length by small scales. Dorsal scales in 19–19–17 rows, strongly keeled, outer row slightly less so; apical pits present throughout body length;

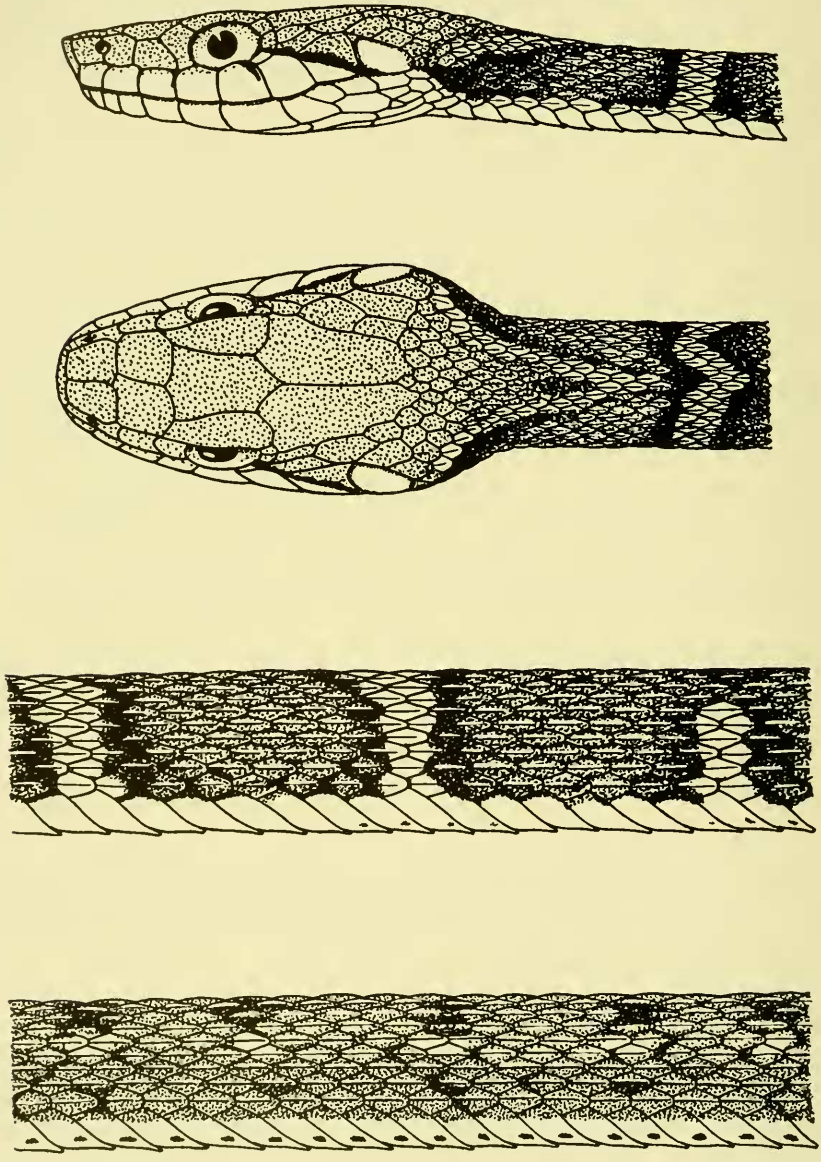

Figure 2. Holotype of *Natrix pryeri ishigakiensis*, CAS 21913. Dorsal and lateral aspects of the head, and lateral view of an anterior and posterior portion of the body.

fourth scale row present for 63.6% of head and body length. Ventrals 174; anal divided; subcaudals 102.

Anterior body with broad dark (gray) blotches, black-edged; separated by narrow (1½ scales wide) vertical, light bars extending from ventrals to vertebral line; first pair meet, forming ring, second and third pairs encircle vertebral dark spot, fourth pair separated partially by vertebral dark spot; reduction of vertical light bars begins with fifth pair, starting first at vertebral line and more posteriorly from ventrals also; posterior half of body with light color reduced to series of dorsolateral spots on fourth to sixth scale rows; dark color bordering blotches anteriorly, reduced posteriorly to dark spots below dorsolateral light series and irregular transverse bars across back; dark dorsal scales with light keels. Chin and throat immaculate; series dark spots along outer edges of ventrals beginning at about thirty-fifth ventral (few scattered small spots anterior to this point), increasing in prominence posteriorly, irregular under tail; outer edges ventrals and subcaudals suffused with dark color of flanks. Head uniformly pale above to nuchal crescent; supralabials white, second to fifth with narrow, short, dark streaks at posterior sutures; dark streak from postoculars to lip at juncture of seventh to eighth supralabials; eighth supralabial white, finely edged dark; nuchal crescent narrow, well-defined, dark along posterior edge, each side extending posteriorly on neck for short distance before converging, a dark spot in angle of "Y" thus formed.

MEASUREMENTS AND PROPORTIONS. Total length 932 mm.; tail 254 mm. Tail/total length ratio: 0.273. Head length/body length ratio: 0.043; head length/width ratio: 1.9; snout 38% head length; eye diameter, projected forward, reaches midnostril point (eye diameter/head length ratio: 0.17).

DENTITION. Maxillary teeth 24–25, in continuous series, last two strongly enlarged. Palato-pterygoid series of teeth 15 plus 30, gradually decreasing in size posteriorly in the series. Dentary teeth 30–30, somewhat larger anteriorly.

HEMIPENES. Hemipenes unforked, extend to level of sixth subcaudal plate; organ spinous, distal spines small, the spines increasing in size basally on organ; one enlarged basal spine; basal area of organ furrowed. Sulcus spermaticus not forked, extending to organ tip; lips spinous.

VARIATION. Variation in scale characters in the paratypes is summarized in table I (see Ishigaki). In pattern they are typical except for minor variations. In CAS 21914 all of the light vertical bars are separated vertebrally, and there is a series of small, dark, light-edged, diamond-shaped figures along the vertebral line on the neck; in CAS 21912 the vertical bars alternate on each side of the body.

Discussion. Interpopulation variation exhibited by *Natrix pryeri* appears to be closely correlated with the geological history of the Riukiu archipelago. Hanzawa *(op. cit.)* has summarized the geological history of the islands (see also, Inger, 1947). The main points outlined by Hanzawa are followed here as a guide to interpreting the pattern of variation set forth above.

The ancestral stock of *N. pryeri* is presumed to have arrived in the Riukiu Islands from the Asian continent via Formosa. Dispersal through the islands probably took place during a period of maximum land emergence, such as occurred during the late Pliocene when the Riukiu archipelago formed one continuous island narrowly separated from the mainland. Competition in the new region may have been present originally (two other forms of *Natrix* have attained Formosa, *N. sauteri,* a form related to *N. pryeri,* and *N. piscator,* an extremely vagile form). Such competition as may have existed apparently was not an effective deterrent, for it is evident that "pro-*pryeri*" (or "*pryeri*") spread throughout the region to the exclusion of its congeners. Submergence of the Riukiu Cordillera and subsequent emergence, to a lesser degree than in Pliocene times, certainly must have initiated breaks in the previously continuous population. Again, in the early-middle Pleistocene, inundation of some subaerial land masses resulted in the isolation of populations of *N. pryeri* on Amami, Okinawa, and in the Yaeyama group. Subsequent emergence united the islands in each group permitting the populations to expand to a limited degree. More recently, slight raising of sea level has produced the contemporary geography of the Riukius and isolated *N. pryeri* on several of the islands.

In the outline above, time of dispersal of "pro-*pryeri*" stock through the Riukiu Islands is highly problematical. However, a late Pliocene dispersion at a time when a continuous land mass was available, is thought to be the most logical for a terrestrial animal such as *N. pryeri.* Emergence of land during early Pleistocene times was nearly as great, with the islands of each group united. At such a time waifing could have proved highly successful as a means of dispersion. The occurrence of *N. pryeri* on Miyako must be attributed to waifing, presumable from the Yaeyama group. In the past, low-lying Miyako is believed to have been drowned with each submergence, and thus would require recolonization with each emergence. The closeness of the Yaeyama group (approximately 60 miles to the south) and the prevailing wind and current directions (south to north) virtually precludes colonization by waifing from any source other than the Yaeyama group. (Unfortunately, the Miyako population is very poorly known and its relationships cannot be determined.)

It is not possible to determine exactly what factors influenced the development of the genetic systems represented by *N. pryeri pryeri* and the

divergent *N. p. ishigakiensis*. Four stages are definable in their evolutionary history: 1) initial dispersion; 2) extreme reduction and isolation of at least three subpopulations; 3) moderate dispersal and expansion of these; 4) recurrence of reduction and isolation (contemporary conditions). In spite of this history of expansion and contraction, and continuous or near-continuous and isolated populations, genetic divergence has not been great (assuming that phenotypic variation is an expression of genetic variation), except in the southern population where isolation is greatest. Interisland variation may be the result of random genetic drift in small isolated populations (the Sewell Wright effect). Populations on Okinawa and Amami are presumed to be relatively large, those on Miyako, Ishigaki, and Iriomote may be smaller. The greater genetic divergence in the more isolated (from other *N. pryeri* populations) southern islands could reflect random drift. Drift may have been effective in establishing the characteristics of the gene pool of the various populations during the periods of isolation. With expansion, particularly in the northern populations where the pools may have been at least partially combined, natural selection pressure would be effective in maintaining certain limitations to the enlarged pools. In the northern populations *(N. pryeri)* random drift would seem to have been rendered virtually impotent by ease of immigration between the islands leaving natural selection as the primary factor acting upon the evolving populations. In the south *(N. p. ishigakiensis)*, whether or not the populations are smaller, drift may have had considerable effect in producing the gene pool on which natural selection is now a maintaining force. Dobzhansky and Pavlovsky (1957) have demonstrated the probability that both random drift and natural selection interact to produce new genetic systems in isolated populations. In the species *N. pryeri* each of these factors may have contributed to establishing and maintaining divergence; however, each appears to have played a somewhat more important role in different areas of distribution.

Natrix pryeri is related to a group of *Natrix* in eastern Asia including *N. vibakari* in Japan, and *N. craspedogaster, N. popei* and *N. sauteri* in southern China. The characteristics of *N. pryeri* suggest that it is a primitive type, in correlation with its isolated, peripheral geographical position. It cannot successfully be derived directly from any of its contemporaries. Although it is closest to *N. craspedogaster* it is presumed to have arisen from a prototype of the group which perhaps ranged broadly in eastern Asia.

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